HOW SPIDER ANATOMY AND THREAD CONFIGURATION SHAPE THE STICKINESS OF CRIBELLAR PREY CAPTURE THREADS

Brent D. Opell: Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0406 USA. E-mail: bopell@vt.edu

ABSTRACT. Cribellar threads are primitive prey capture threads formed of thousands of fine, looped cribellar fibrils that surround larger, supporting fibers. Cribellar fibrils are produced from the spigots of an abdominal spinning field, the cribellum, which may be either a single, oval plate or a pair of medially divided plates. The number of spigots on a spider's cribellum is known to be directly related to the stickiness of its cribellar thread. Some spiders deposit cribellar threads in their webs as taut, self-supporting linear threads; others deposit looped threads along a supporting foundation thread. This study showed that the looped cribellar threads of *Kukulcania hibernalis* (Filistatidae) and *Mexitlia trivittata* (Dictynidae) were wider and stickier than linear threads produced by *Waitkera waitakerensis* and *Uloborus glomosus* (Uloboridae), respectively, that had the same numbers of cribellum spigots. Linear cribellar thread spun from the divided cribellum of *K. hibernalis* was both wider and stickier than linear thread spun from the undivided cribellum of *W. waitakerensis* that had the same number of spigots. A single cribellar plate of *K. hibernalis* and the cribellum of *Siratoba referena* (Uloboridae) had a similar number of spigots and produced cribellar threads with similar stickiness. Thus, both a spider's spinning anatomy and its spinning behavior affect the stickiness of its cribellar threads.

Keywords: Cribellum, spigot number, thread stickiness

Many spiders increase the effectiveness of their capture webs by incorporating sticky prey capture threads that slow or prevent the escape of insects from the web, thus giving a spider more time to subdue prey. These threads are of two types: dry, fuzzy cribellar capture threads (Eberhard & Pereira 1993; Opell 1994a, 1995, 1996, 1999a; Peters 1983, 1984, 1986) and viscous, adhesive threads (Opell 1997, 1998; Peters 1995; Tillinghast et al. 1993; Townley et al. 1991; Vollrath 1992; Vollrath et al. 1990; Vollrath & Tillinghast 1991). Cribellar threads are present in aerial webs constructed by the basal members of the large Infraorder Araneomorphae (Forster et al. 1987; Platnick 1977), whereas adhesive threads first appeared in the Araneoidea clade that includes modern orb-weaving spiders (Bond & Opell 1998; Coddington & Levi 1991).

The outer surfaces of cribellar threads (Figs. 1–3) are formed of thousands of fine, looped fibrils. These fibrils are spun from spigots on an oval spinning field termed the cribellum that is borne on the ventral surface of a spider's abdomen (Figs. 4–6; Kovoor & Peters 1988; Opell 1994b, 1999a; Peters 1992). Fibrils are drawn from the cribellar spigots by a setal comb termed the calamistrum that is located on the metatarsus of each fourth leg (Eberhard 1988; Opell 1994b, 1995, 1999a; 2001; Opell et al. 2000; Peters 1983, 1984, 1986). Rhythmic adductions of the posterior lateral spinnerets form the sheet of cribellar fibrils around supporting axial and auxiliary fibers to form a cribellar thread (Peters 1984) that often appears as a series of torus-shaped puffs (Fig. 1; Eberhard & Pereira 1993). Cribellar threads are still produced by representatives of all major araneomorph clades (Griswold et al. 1999) and are found in webs whose architectures range from sheet- and funnel-webs to cob-webs and orb-webs (Opell 1999). However, many araneomorph spiders have lost the cribellum and, with it, the ability to produce cribellar thread.

Cribellar threads are deposited in both their initial linear form and in a looped form (Fig. 1 and Figs. 2–3, respectively; Eberhard & Pereira 1993; Opell 1990, 1999a; Peters 1984, 1992). Linear threads are typically taut, self-supporting threads that run between non-
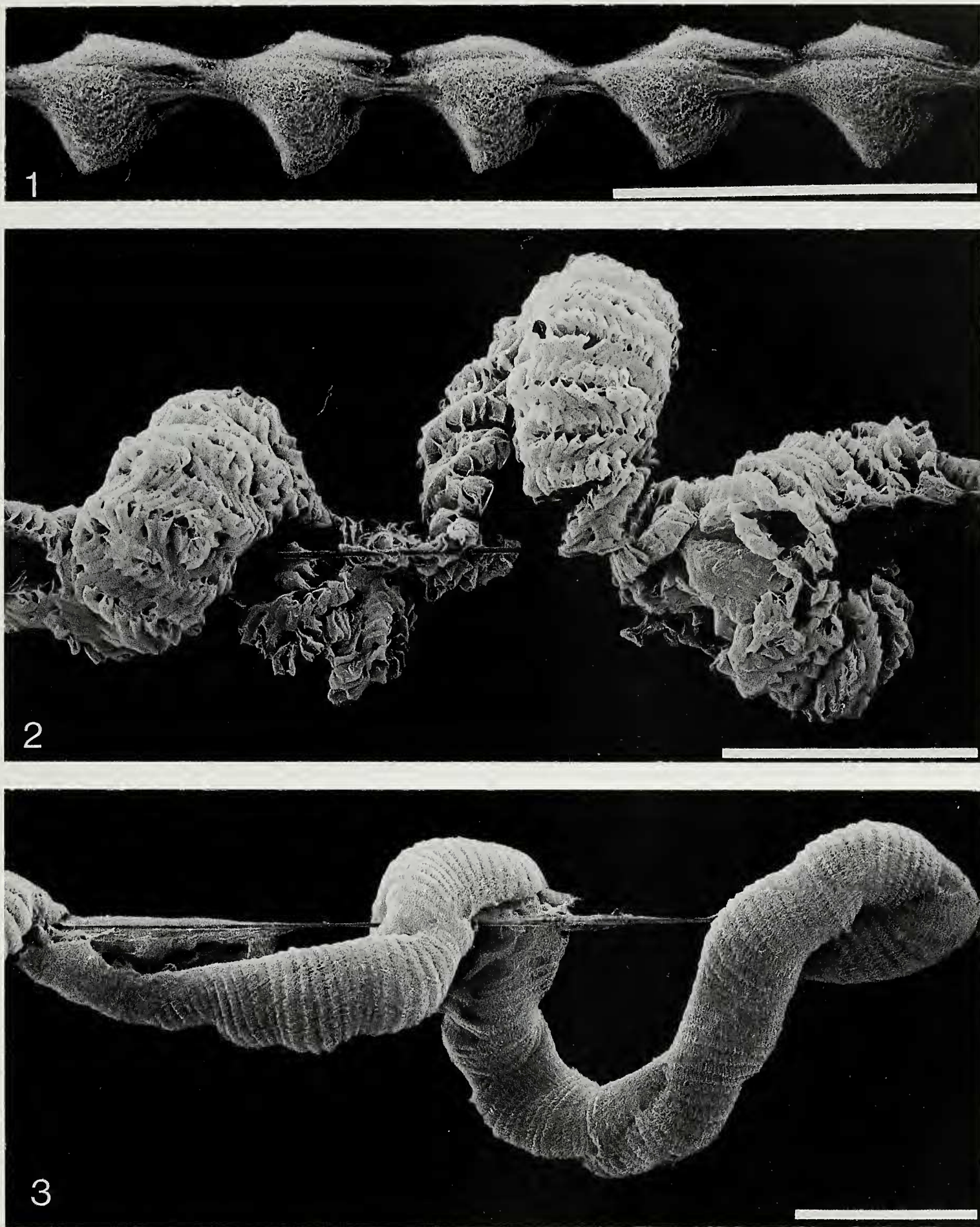
Figures 1–3.—Cribellar threads. 1. Linear thread of *Waitkera waitakerensis*; 2. Looped thread of *Kukulcania hibernalis*; 3. Looped thread of *Mexitlia trivittata*. Scale bars are 400 μm long.

sticky lines, such as the spirals of orb-webs produced by members of the spider family Uloboridae. However, in some webs they are deposited along a supporting non-sticky line, although usually for only short distances (Eberhard 1987; Opell 1982, 1990; Peters 1983, 1992). In contrast, looped threads are always laid down on non-sticky foundation lines that have been previously deposited (Eberhard 1988; Lubin et al. 1978). This makes it possible for a spider to fold and loop a strand of cribellar thread as it is being
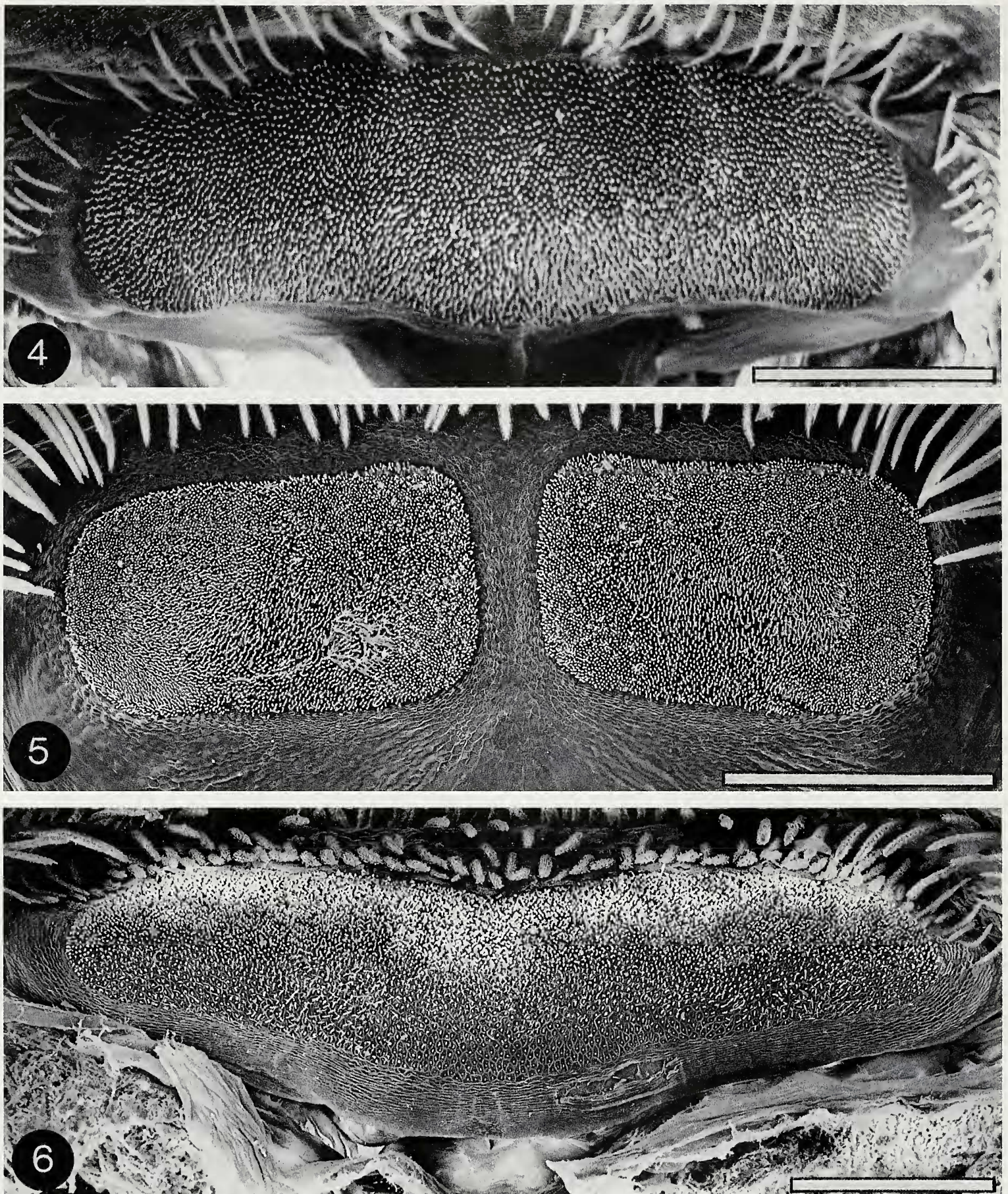
Figures 4–6.—Cribella. 4. Cribellum of *Waitkera waitakerensis*; 5. Cribellum of *Kukulcania hibernalis*; 6. Cribellum of *Mexitlia trivittata*. Scale bars are 100 μm long.

pressed against the foundation line, and probably shifts much of the thread's support from its own axial and auxiliary fibers that lie within, to the foundation line on which the looped thread is placed.

There is an evolutionary premium on the stickiness of capture threads. An increase in the stickiness of linear cribellar thread was as-

sociated with the origin of orb-weaving spiders from non-orb-weavers (Opell 1999a) and with the reduction of the orb-web within the genera *Hyptiotes* Walckenaer 1837 and *Miagrammopes* O. Pickard-Cambridge 1869 of the family Uloboridae (Opell 1994a, b). The evolutionary replacement of cribellar threads by adhesive capture threads in the Araneoidea

was also associated with an increase in thread stickiness (Opell 1997, 1998, 1999b). Interspecific comparisons of linear cribellar threads show that cribellar thread width is also directly related to thread stickiness (Opell 1995).

These findings suggest that the spinning behavior that produces looped cribellar thread (Figs. 2–3) may be an alternative mechanism for increasing thread stickiness. By reconfiguring the native linear thread, this behavior increasing the thread's effective width, allowing it to present more cribellar fibrils per mm length to an insect surface. Thus, the stickiness of a looped cribellar thread should be greater than that predicted by the number of spigots on the spider's cribellum or by the width of its cribellum. To test this hypothesis, I compared the stickiness and widths of looped and linear cribellar threads produced by spiders with similar numbers of spigots on their cribella.

METHODS

Species studied.—*Kukulcania hibernalis* (Hentz 1842) (Family Filistatidae) occupies a silk-lined cavity from which a network of capture threads radiate, typically suspended a few mm to a cm above the substrate. *Mexitlia trivittata* (Banks 1901) (Family Dictynidae) constructs a silken retreat on low vegetation, logs, or other supports and spins a series of often long capture lines that radiate from the retreat. Both species produce looped cribellar threads (Figs. 2 & 3, respectively). *Waitkera waitakerensis* (Chamberlain 1946), *Uloborus glomosus* (Walckenaer 1837), and *Siratoba referena* (Muma & Gertsch 1964) belong to the Family Uloboridae and construct orb-webs. Webs of the first two species are typically horizontal, whereas those of the latter may be built at greater angles. These three species produce linear cribellar threads (Fig. 1).

Unlike the other species included in this study, *K. hibernalis* has a divided cribellum (Fig. 5). This, and the fact that its cribellar thread can be artificially reconfigured, make it a pivotal species for this study. The fibrils from each cribellar plate remain distinct as they are combed by the calamistrum and, in contrast to the looped cribellar thread of *M. trivittata*, that of *K. hibernalis* can be separated from the foundation line on which it rests and returned to a linear configuration.
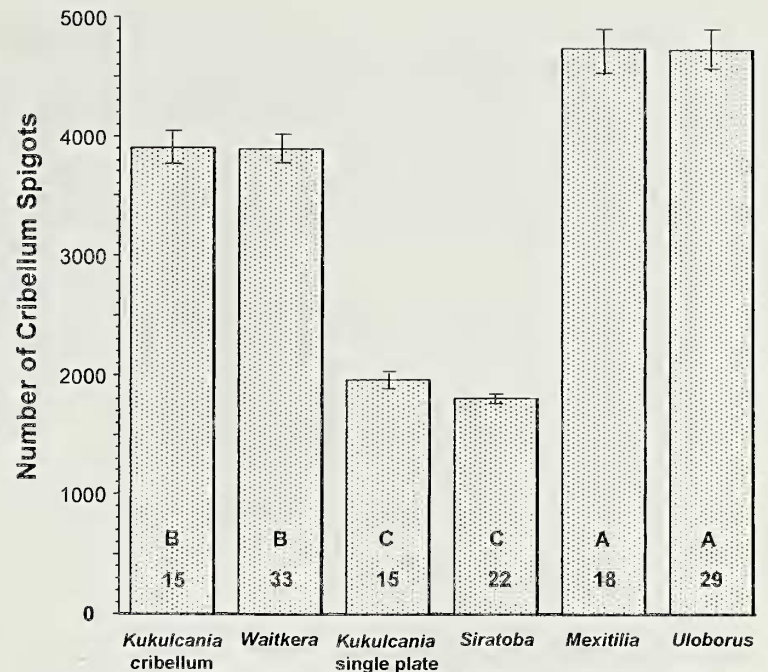

Figure 7.—Comparison of cribellar spigot number. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

The linear thread can then be separated into two strands, each formed of cribellar fibrils produced by one of the two cribellar plates. *Kukulcania hibernalis* and *W. waitakerensis* have similar numbers of cribellum spigots and the number of spigots on the cribellum of *S. referena* is similar to that on a single cribellar plate of *K. hibernalis* (Fig. 7). *Mexitlia trivittata* and *U. glomosus* have similar numbers of cribellar spigots (Fig. 7). Consequently, it is possible to make the three comparisons of cribellar thread stickiness shown in Table 1.

Only adult females were included in this study. The sample sizes for cribellum features, thread measurements, and thread stickiness values are given in Figures 7–11. For each species the same set of individuals was used for all the measurements, although for a few individuals not all measurements were available. Only one stickiness value per thread configuration per individual was included. I studied *K. hibernalis* at the Archbold Biological Station near Lake Placid, Florida; *M. trivittata* and *S. referena* at the American Museum of Natural History's Southwestern Research Station near Portal, Arizona; *U. glomosus* near Blacksburg, Virginia, and *W. waitakerensis* near Whangarei, New Zealand. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology.

Cribellum features.—I removed the cri-

Table 1.—Comparisons of the stickiness of cribellar threads and strands produced by cribella or cribellar plates with similar numbers of spigots.

Comparison	Species
Looped and linear cribellar threads	*Kukulcania hibernalis* vs. *Waitkera waitakerensis* *Mexitilia trivittata* vs. *Uloborus glomosus* *Kukulcania hibernalis* looped vs. linear.
Threads produced from entire and divided cribella	*Waitkera waitakerensis* vs. *Kukulcania hibernalis*
Threads produced from a single cribellar plate of a divided cribellum and an entire cribellum.	*Kukulcania hibernalis* vs. *Siratova referena*

bella of species whose thread features were measured, mounted them in water-soluble medium on microscope slides, and examined them under a compound microscope equipped with differential phase contrast (Nomarski) optics. For the divided cribella of *K. hibernalis*, I measured cribellum width as the distance between the lateral edges of the two cribellar plates. I included the space between the plates in this measurement because this is the functional width of the cribellum.

For the entire cribella of *M. trivittata, W. waitakerensis, S. referena*, and *U. glomosus*, I used a video camera and a computerized digitizing apparatus to measure the surface area of the cribellum and the density of approximately 50 spigots in each of three regions of the cribellum: anterior midline, lateral central region, and posterior lateral margin. I computed the number of cribellum spigots by multiplying surface area by mean spigot density. For the divided cribella of *K. hibernalis*, I measured the area of a single cribellar plate and determined the density of spigots in the median, central, and lateral regions of this plate. I doubled the number of spigots on a single plate to obtain the total number of cribellum spigots.

Cribellar thread features.—I collected cribellar threads from webs on microscope slides to which raised supports were glued. Double sided tape atop each support secured the thread at its native tension. The supports on thread samplers used for stickiness measurements were glued at 4.8 mm intervals. The thread widths of the three uloborid species were measured at 100 X under a compound microscope. *Kukulcania hibernalis* threads were measured at 25 X under a dis-

secting microscope and *M. tivittata* were measured at 40 X under a compound microscope.

I measured the stickiness of only recently spun threads that were not contaminated by dust or pollen, or damaged by a spider walking on them. These were collected from newly constructed orb-webs and from newly deposited capture lines of non-orb-weaving species. In the latter case, this was facilitated by partially destroying a web and looking each morning for new threads. I measured thread stickiness with a strain gauge that incorporates a glass or stainless steel needle (Opell 1993; 1994a). A contact plate made from a 2 mm wide piece of 320 grit, 3M® waterproof silicon carbide sandpaper was glued to the tip of this needle. The particles on the surface of these sandpaper plates are uniform in size and distribution (Opell 1993) and these plates registered the same stickiness for cribellar threads as did contact plates made from sarcophagid fly wings (Opell 1994a). Thus, a sandpaper contact plate registers stickiness values similar to that of a representative insect surface.

A motorized advancement mechanism pressed the cribellar thread against a sandpaper contact plate at a constant speed (13.5 mm/min for threads from uloborids and 10.7 mm/min for the other two species) until a force of 19.61 μN/mm of thread contact was achieved. The thread was then immediately withdrawn by this mechanism at a constant speed (14.0 mm/min for threads of uloborids and 10.4 mm/min for threads of the other two species) until it pulled free from the plate. The force registered by the strain gauge immediately before this occurred was divided by the contact plate's width (measured to the nearest 20 μm) to yield stickiness, expressed as μN
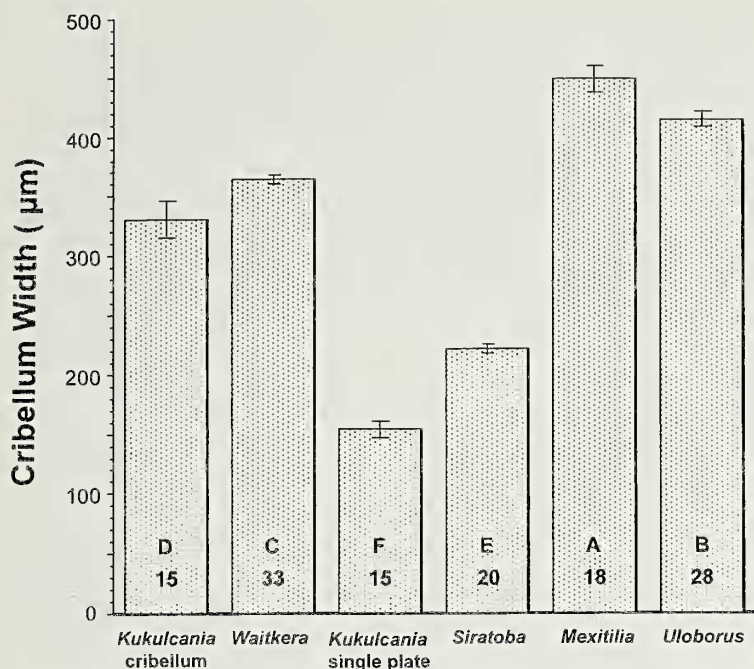
Figure 8.—Comparison of cribellum width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

Figure 9.—Comparison of cribellar thread width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

of force per mm of thread contact with the sandpaper plate. The stickiness of four thread samples was measured for each specimen or, in the case of *K. hibernalis*, for each thread configuration, and their mean used as a spider's value.

Statistical analysis.—The normality of data was tested with a Shapiro-Wilk W-statistic (SW). I used a one way analysis of variance test (ANOVA) to determine if features differed among groups and a Ryan-Einot-Gabriel-Welsch multiple range test with alpha = 0.05 (RGW, Day & Quinn 1989) to rank the values of features. These tests were performed with SAS for the Power Macintosh Computer (SAS Institute, Cary, North Carolina).

RESULTS

The number of spigots on each species' cribellum and on the single cribellar plate of *K. hibernalis* was normally distributed (SW $P >$ 0.26). The means of these groups differed (ANOVA $F = 112.29$, $P = 0.0001$) and an RGW test (Fig. 7) supported the pairing of species described in Table 1. Cribellum width was also normally distributed for these groups (SW $P > 0.13$) and relationships among the groups' values (Fig. 8) reflect those of spigot number.

Thread width was not normally distributed for all groups. However, when log transformed it became so (SW $P > 0.07$) for all
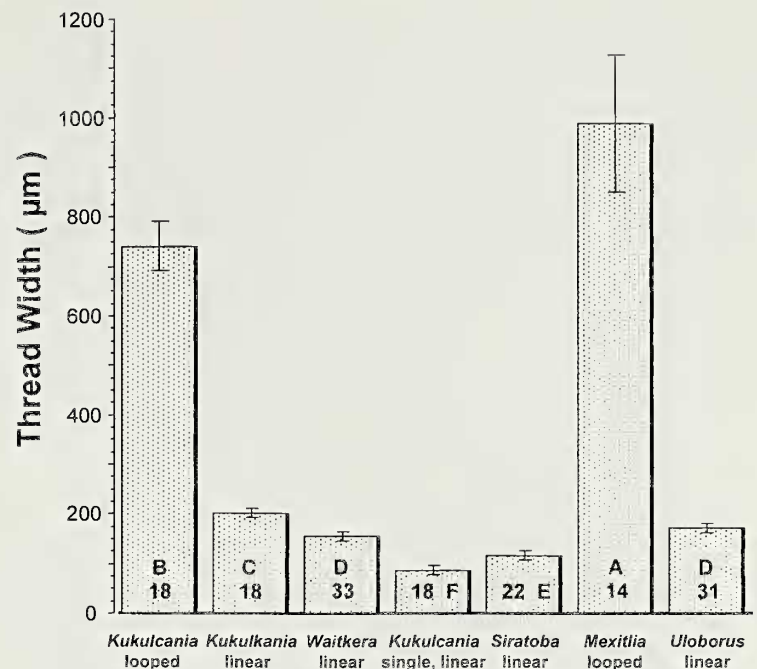
groups but the single threads of *K. hibernalis*. These values could not be normalized, as 16 of the 18 values were identical. Transformed values differed among groups (ANOVA $F = 375.62$, $P = 0.0001$). An RGW test showed that the looped threads of *K. hibernalis* and *M. trivittata* were much wider than the linear threads produced by *W. waitakerensis* and *U. glomosus*, respectively, that had the same number of cribellum spigots (Fig. 9). The linear threads of *K. hibernalis*, *W. waitakerensis*, and *U. glomosus* had the greatest widths, and single-stranded threads of *K. hibernalis* and linear threads of *S. referena* had the smallest widths.

The ratio of cribellar thread width to cribellum width was not normal for all groups, but became so when log transformed (SWP $P > 0.18$). Transformed values differed among species (ANOVA $F = 41.79$, $P = 0.0001$). Their RGW rankings (Fig. 10) show that the looped threads of *K. hibernalis* and *M. trivittata* had a ratio of about 2.3, whereas single- and double-stranded threads of *K. hibernalis* and the linear threads of *W. waitakerensis*, *S. referena*, and *U. glomosus* had values that fell in the narrow range of 0.4–0.6.

Thread stickiness was not normally distributed for all groups but became so when log transformed (SW $P > 0.08$). Transformed values differed among species (ANOVA $F = 50.94$, $P = 0.0001$) and their RGW rankings
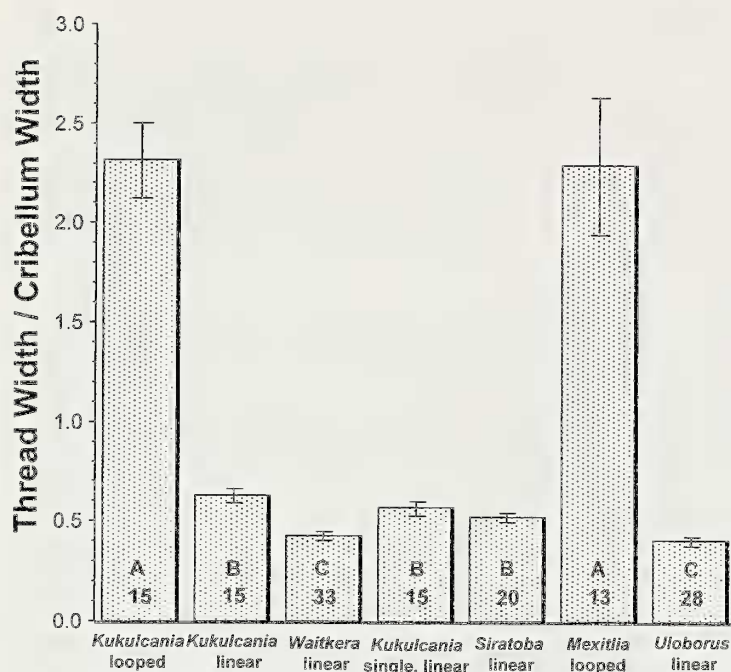
Figure 10.—Comparison of the ratio of cribellar thread width to cribellum width. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test.

Figure 11.—Comparison of cribellar thread stickiness. Error bars denote ± 1 standard error. Sample sizes are given at the bases of histogram bars. Letters within histogram bars denote rankings of a Ryan-Einot-Gabriel-Welsch multiple range test for all comparisons. Underlined letters rank the stickiness of the five linear cribellar strands and threads.

(Fig. 11, non-underlined letters) reflected those of thread widths. Looped cribellar threads of *K. hibernalis* and *M. trivittata* had the greatest stickiness, and the stickiness of double- and single-stranded *K. hibernalis* threads matched most closely those of *W. waitakerensis* and *S. referena*, respectively, with similar thread widths and similar numbers of cribellum spigots. When looped threads of *K. hibernalis* and *M. trivittata* were excluded, differences remained significant (ANOVA $F = 10.70$, $P = 0.0001$) and their RGW rankings (Fig. 11, underlined letters) showed that the stickiness of single-stranded *K. hibernalis* thread and *S. referena* thread had the same stickiness. However, the stickiness of double-stranded *K. hibernalis* thread exceeded that of the naturally linear thread of *W. waitakerensis*.

DISCUSSION

The results of this study show that a spider greatly increases the stickiness of its cribellar thread by depositing it in a looped fashion. The stickiness of linear cribellar thread is determined mainly by the number of spigots on a spider's cribellum (Opell 1994b, 1999a), whereas the stickiness of looped thread is shaped by a spider's spinning behavior. The looped threads of *K. hibernalis* are 2.1 times stickier than the linear threads of this species and 3.0 times stickier than the linear threads
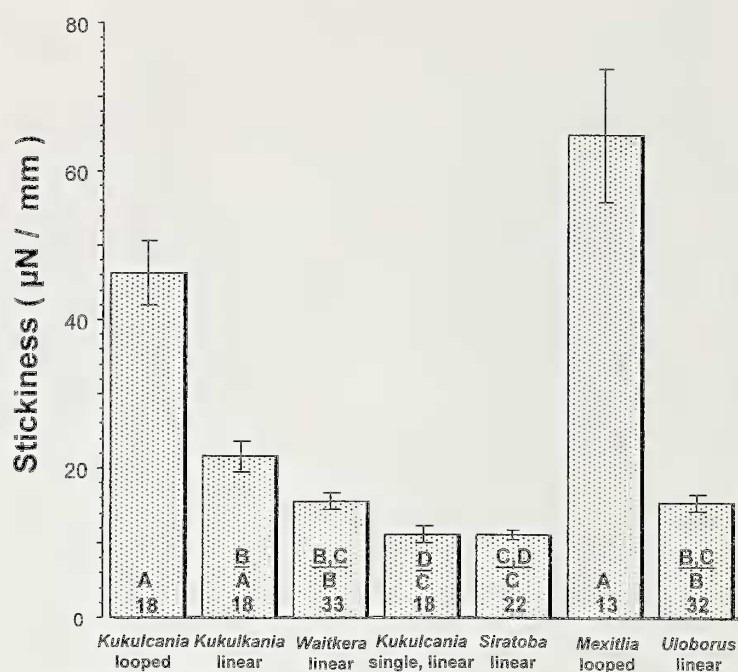
of *W. waitakerensis*, whose cribellum bears the same number of spigots. The looped threads of *M. trivittata* are 4.2 times stickier than the linear threads of *U. glomosus*, whose cribellum has the same number of spigots.

Among spiders that produce linear cribellar threads (or in the case of *K. hibernalis*, threads that can be made linear) thread stickiness mirrors thread width (Figs. 8 & 9). A formal analysis of this relationship is not possible due to the limited taxonomic representation and small sample size of this study and the inclusion of two types of artificially produced linear threads of *K. hibernalis*. However, positive Pearson correlations for thread width and thread stickiness among the seven threads studied ($r = 0.99$, $P = 0.0001$) and among the five linear threads ($r = 0.93$, $P = 0.02$) lend support to the hypothesis that cribellar thread width is an important determinant of thread stickiness.

The cribellum is a synapomorphy of the large Infraorder Araneomorphae (Forster et al. 1987; Platnick 1977) and first appeared as a single oval plate. A divided cribellum is found in a number of araneomorph taxa, and cribellum division appears to be a rather plastic trait. For example, in the genus *Mallos* O. Pickard-Cambridge 1902, the sister genus of *Mexitlia* Lehtinen 1967 (Bond & Opell

1997a), the plesiomorphic state is an undivided cribellum. However, in this clade of 14 species a terminal subclade of six *Mallos* species has as one of its synapomorphies a divided cribellum. Within this *Mallos* subclade, the divided cribellum has been reversed to a single plate in two sister species (Bond & Opell 1997b).

The relationship between cribellum width and cribellar thread stickiness may help explain the advantage of the divided cribellum of spiders like *K. hibernalis* (Fig. 5). By increasing the lateral spread of a cribellum's spigots, the divided condition may produce wider bands of cribellar fibrils that, when formed around supporting threads, produce wider and, therefore, stickier cribellar threads. Tentative support for this hypothesis comes from a comparison of the thread width, thread width/cribellum width ratio, and thread stickiness values of linear (double-stranded) *K. hibernalis* threads and *W. waitakerensis* threads (Figs. 9–11). These two species have cribella with the same number of spigots (Fig. 7), yet the linear thread of *K. hibernalis* has a greater thread width, thread width/cribellum width ratio, and stickiness than does *W. waitakerensis*. As the linear threads of *K. hibernalis* were produced by manipulating the spider's native looped cribellar threads, this conclusion must be interpreted cautiously and should be confirmed by studies of species that possess divided cribella and produce linear cribellar threads.

A different conclusion about the effect of cribellum division upon thread stickiness was reached by Bond & Opell (1997b). In a phylogenetic study that included four *Mallos* species with undivided cribella and two species with divided cribella, they found that cribellum width, surface area, and spigot number of all six species was directly related to carapace width. As cribellar thread stickiness is known to be related to cribellar thread width (Opell 1995) and cribellar spigot number (Opell 1994b), these authors found no support for the hypothesis that species with divided cribella produce stickier cribellar threads than species with undivided cribella. Although this and the present study draw conflicting conclusions about the effect of cribellar division on cribellar thread stickiness, neither resolves the question definitively.

Increasing cribellar thread stickiness re-

quires an increased silk investment. This may be achieved by increasing the number of fibrils that form a linear thread or by increasing the amount of linear thread that is folded to form a looped thread. Adult female *K. hibernalis* have a mass that is 37.2 times that of *W. waitakerensis* and adult female *M. trivittata* a mass that is 2.2 that of *U. glomosus* (Opell 1999a). Consequently, it is clear that spider size does not limit the number of spigots that a cribellum can bear and thus does not require a spider to produce looped threads in order to achieve greater thread stickiness. A number of non-orb-weaving spiders also produce linear cribellar threads (Opell 1999a), so web architecture also fails to provide a simple explanation for these two approaches. The prey capture performances of looped and linear threads probably differ more substantially than indicated by the stickiness measured in this study. Looped threads may be better adapted to fold around the appendages of an insect and, thus, achieve a greater area of contact than taut linear threads (Lubin et al. 1978). As insects struggle, loops may stretch and pull free from their foundation lines, helping to absorb some of the force generated by a struggling insect and making it more likely that the insect will contact other looped threads (Eberhard 1976; Opell 1990).

ACKNOWLEDGMENTS

LITERATURE CITED

Bond, J.E. & B.D. Opell. 1997a. Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae, Dictynidae). Zoological Journal of the Linnean Society 119:389–445.

Bond, J.E. & B.D. Opell. 1997b. The functional significance of medially divided cribella in the spider genus *Mallos* (Araneae, Dictynidae). Bulletin

of the British Arachnological Society 10:239–241.

Bond, J.A., & B.D. Opell. 1998. Testing adaptive radiation and key innovation hypotheses in spiders. Evolution 52:403–414.

Coddington, J.A. & H.W. Levi. 1991 Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22:565–592.

Day, R.R. & G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.

Eberhard, W.G. 1976. Physical properties of sticky spirals and their connections: sliding connections in orb webs. Journal of Natural History 10:481–488.

Eberhard, W.G. 1987. Construction behaviour of non-orb weaving cribellate spiders and the evolutionary origin of orb webs. Bulletin of the British Arachnological Society 7:175–178.

Eberhard, W.G. 1988. Combing and sticky silk attachment behavior by cribellate spiders and its taxonomic implications. Bulletin of the British Arachnological Society 7:247–251.

Eberhard, W.G. & F. Pereira. 1993. Ultrastructure of cribellate silk of nine species in eight families and possible taxonomic implications (Araneae: Amaurobiidae, Deinopidae, Desidae, Dictynidae, Filistatidae, Hypochilidae, Stiphidiidae, Tengellidae). Journal of Arachnology 21:161–174.

Forster, R.R., N.I. Platnick, & M.R. Gray. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae. Bulletin of the American Museum of Natural History 185:1–116.

Griswold, C.W., J.A. Coddington, N.I. Platnick, & R.R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). Journal of Arachnology 27:53–63.

Kovoor, J. & H.M. Peters. 1988. The spinning apparatus of *Polenecia producta* (Araneae, Uloboridae): Structure and histochemistry. Zoomorphology 108:47–59.

Lubin, Y.D., W.G. Eberhard, & G.G. Montgomery. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche 85:1–23.

Opell, B.D. 1982. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). Bulletin of the British Arachnological Society 5:338–343.

Opell, B.D. 1990. Material investment and prey capture potential of reduced spider webs. Behavioral Ecology and Sociobiology 26:375–381.

Opell, B.D. 1993. What forces are responsible for the stickiness of spider cribellar threads? Journal of Experimental Zoology 265:469–476.

Opell, B.D. 1994a. Increased stickiness of prey capture threads accompanying web reduction in the spider family Uloboridae. Functional Ecology 8:85–90.

Opell, B.D. 1994b. Factors governing the stickiness of cribellar prey capture threads in the spider family Uloboridae. Journal of Morphology 221:111–119.

Opell, B.D. 1995. Ontogenetic changes in cribellum spigot number and cribellar prey capture thread stickiness in the spider family Uloboridae. Journal of Morphology 224:47–56.

Opell, B.D. 1996. Functional similarities of spider webs with diverse architectures. American Naturalist 148:630–648.

Opell, B.D. 1997. The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. Biological Journal of the Linnean Society 62:43–458.

Opell, B.D. 1998. Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. Functional Ecology 12:613–624.

Opell, B.D. 1999a. Changes in spinning anatomy and thread stickiness associated with the origin of orb-weaving spiders. Biological Journal of the Linnean Society 68:593–612.

Opell, B.D. 1999b. Redesigning spider webs: stickiness, capture area, and the evolution of modern orb-webs. Evolutionary Ecology Research 1:503–516.

Opell, B.D. 2001. Cribellum and calamistrum ontogeny in the spider family Uloboridae: linking functionally related but separate silk spinning features. Journal of Arachnology 29:220–226.

Opell, B.D., J.S. Sandidge, & J.E. Bond. 2000. Exploring functional associations between spider cribella and calamistra. Journal of Arachnology 28:43–48.

Peters, H.M. 1983. Struktur und Herstellung der Fangfäden cribellater Spinnen (Arachnida: Araneae). Verhandlungen des naturwissenschaftlichen Vereins, Hamburg 26:241–253.

Peters, H.M. 1984. The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida, Araneida). Zoomorphology 104:96–104.

Peters, H.M. 1986. Fine structure and function of capture threads. Pp. 187–202, *In* Ecophysiology of Spiders (W. Nentwig, ed.). Springer Verlag, New York.

Peters, H.M. 1992. On the spinning apparatus and structure of the capture threads of *Deinopis subrufus* (Araneae, Deinopidae). Zoomorphology 112:27–37.

Peters, H.M. 1995 Ultrastructure of orb spiders' gluey capture threads. Naturwissenschaften 82:380–382.

Platnick, N.I. 1997. The hypochiloid spiders: a cladistic analysis with notes on the Atypoidea (Aachnida: Araneae). American Museum of Natural History Novitates 2627:1–23.

Tillinghast, E.K., M.A. Townley, T.N. Wight, G.

Uhlenbruck,. & E. Janssen. 1993 The adhesive glycoprotein of the orb web of Argiope aurantia (Araneae, Araneidae). Materials Research Society, Symposium Proceedings 292:9–23.

Townley, M.A., D.T. Bernstein, K.S. Gallanger, & E.K. Tillinghast. 1991 Comparative study of orb-web hydroscopicity and adhesive spiral composition in three areneid spiders. Journal of Experimental Zoology 259:154–165.

Vollrath, F. 1992. Spider webs and silks. Scientific American 266:70–76.

Vollrath, F., W.J. Fairbrother, R.J.P. Williams, E.K. Tillinghast, D.T. Bernstein, K.S. Gallagher, & M.A. Townley. 1990 Compounds in the droplets of the orb spider's viscid spiral. Nature 345:526–528.

Vollrath, F. & E.K. Tillinghast. 1991 Glycoprotein glue beneath a spider web's aqueous coat. Naturwissenschaften 78:557–559.